Not just for adults! Evaluating the performance of multiple fish passage designs at low-head barriers for the upstream movement of juvenile and adult trout *Salmo trutta*

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Abstract

Longitudinal connectivity in salmonid streams is vital for juvenile as well as adult fish, yet most upstream passage studies consider only larger adults. Upstream passage of juvenile and adult brown trout *Salmo trutta* at low-head (< 3 m) structures on two River Ribble tributaries (NW England) was investigated using Passive Integrated Transponder (PIT) telemetry during summer-autumn 2013 and 2014. The efficiency of a Servais low-cost baffle (LCB) fish pass was evaluated for the first time, along with two pool-weir (PW) passes, an embedded rock ramp (ERR) and an open culvert (C), the latter a man-made structure within predicted swim speed, acting as an experimental control. We used a combination of naturally migrating trout and displacement experiments. Resident fish were displaced from above to below structures, utilising their homing instinct to instigate their ascent of the structure, with up to 91% of displaced trout attempting to pass. Approximately 30% of parr morphotype trout released at their capture locations attempted to pass upstream of structures in both streams. Passage efficiencies of up to 82% for the LCB pass design were similar to the PW (up to 79%) and better than the ERR (71%), but below that for C (96% - 100%). Significant differences occurred between fish passes in time to passage, and number of attempts to pass, with all but PW1 having significantly longer time to passage than the control culvert. Median time to passage at PW2 decreased almost fifty fold between 2013 and 2014, following modification to equalise step heights at the structure. Logistic regression demonstrated a strong body-length effect on passage success at passes, with 50% probability of successful passage (82-132 mm) varying, but not significantly, between passes. We conclude that small trout, including juveniles, can and do exhibit functionally

significant upstream movement and that greater consideration should be given of their passage needs as well as for large, adult trout.

Keywords: *Salmo trutta*, body size, fish passage, PIT telemetry, low-cost baffle, pool-weir, rock ramp, culvert, low-head barrier, delay

1. Introduction

Connectivity is a fundamental element of landscape structure and ecological processes and the longitudinal connectivity dimension is especially important in rivers (Fausch et al., 2002; Taylor et al., 1993). The ecological impacts of impoundment by in-stream structures such as dams, weirs and culverts on river systems can be extensive, especially upon fish populations, altering habitat and creating upstream and downstream obstacles to migration and dispersal (Aarestrup & Koed, 2003; Larinier, 2001; Lucas and Baras, 2001). Loss of free passage due to artificial barriers can lead to habitat fragmentation and limit fish distribution in water courses by reducing access to key habitats such as spawning grounds (Fausch et al., 2002; Lucas et al., 2009). River systems are particularly susceptible to fragmentation (Nilsson et al. 2005; Calles & Greenberg, 2009) as one barrier has the potential to isolate large sections of river from one another (Jager et al., 2001). Where a structure acts as a total barrier to upstream fish passage it can result in stark changes in community structure due to isolation (Pringle et al., 2000; Thorncraft and Harris, 2000). For fish which rely on migration to reach different habitat patches for life-cycle completion, especially diadromous fishes which may need to traverse large numbers of structures on their migration between the sea and freshwater, fragmentation can lead to extinctions upstream of structures (Lucas & Baras, 2001; McDowall, 1992). Loss of longitudinal connectivity can also decrease abundance more widely in the catchment when recruitment is reduced by lack of access to spawning/rearing grounds or due to reduced downstream migration success (Levin & Tolimieri, 2001; McDowall, 1992).

In contrast to high-head dams (> 15 m; Poff and Hart, 2002), the effects of small structures such as low-head dams, weirs and culverts are less well studied (Alexandre and Almeida, 2010; Lucas & Frear, 1997; McLaughlin et al., 2006; Ovidio & Philippart, 2002). While small structures are often considered to be passable by strong swimmers and jumpers like salmonids (McLaughlin et al., 2006) they can still bring about migration delays while they are being negotiated (Svendsen et al., 2004), reducing the condition of spawning fish and increasing exposure to predators. Kiffney et al. (2009) showed that access to small streams was particularly important in the rearing of juvenile salmonids, providing important habitat benefits for growth and survival. The presence of these structures, such as culverts, has been reported to have negative effects on the dispersal (Gibson et al., 2005; Park et al., 2008; Warren and Pardew, 2008) and distribution (Pépino et al., 2012) of fish populations with impacts on genetic diversity similar to those of natural waterfalls (Torterotot et al., 2014).

In order to mitigate the negative effects of obstacles on upstream migration, fish passage technologies have been developed, such that there is now a wide variety of designs, categorised as either technical (e.g. vertical slot, pool and weir, baffle-type) or nature-like (e.g. by-pass channels and rock ramps) (Clay, 1995; Katopodis and Williams, 2012). Evaluation of the performance of fish passage structures has indicated that the degree of success achieved can be very variable and site specific (Kemp, 2012). Even if a high proportion of fish manage to pass using a fishway, negative impacts are often still incurred, including migration delay, with fish attempting to pass structures on multiple occasions (Foulds and Lucas, 2013; Gowans et al., 1999; Haro and Kynard, 1997; Hasler et al., 2011; Laine, 1995; Keefer et al., 2004). The ability to understand the effects of migration delay have been limited by our ability to quantify it (Castro-Santos & Haro, 2003). With 25,000 known man-made barriers on UK rivers alone, and an increased ambition to provide free fish passage, it is important to determine the functionality of fish passage designs (Gough et al., 2012). This is especially true within tributaries where the impacts of barriers are less well investigated than in main stems of rivers where fish passage facilities have mainly been constructed (Clay, 1995; Marmulla & Ingendahl, 1996; Ovidio & Philippart, 2002).

Although fish passes have a long history (e.g. Denil, 1909) there remains a paucity of good quality empirical information about the true effectiveness of differing types of pass for different species of migratory fish (Bunt et al., 2012). Many fish pass designs originated to accommodate adult salmonids with strong swimming capacities and a persistent desire to pass upstream (Stuart, 1962, 1964). However, there is a range in swimming ability present not only across species, but different life stages also, for which passage structures are not always designed to accommodate. Free passage is not only important for adult fishes but can also be vital for juveniles where it is required for them to recover from disturbance events such as displacement by high flows (Ottaway & Clarke, 1981) or pollution incidents (Baras and Lucas, 2001), for the seeking of resources and seasonal shifts in distribution (Baras and Lucas, 2001), or where juvenile morphotypes mature (e.g. male precocious salmonid parr) and contribute towards population survival through alternative spawning strategies (Garcia-Vazquez et al., 2001).

In order to achieve effective fish passage solutions that allow free migration and assist in lifecycle completion, better quality information is required as to the performance of fish pass designs. This study used passive integrated transponder (PIT) technology (Castro-Santos et al., 1996; Lucas et al., 1999; Calles & Greenberg, 2005; Bunt et al., 2012; Foulds & Lucas, 2013) to evaluate the performance of three types of low-head fish pass (pool-weir, rock ramp, low-cost baffle) for the upstream passage of both adult and juvenile brown trout (*Salmo trutta*) utilising both natural migration and in-nature displacement experiments. The current study includes the first quantitative evaluation of the low-cost baffle design of Servais (2006) that is increasingly being used in the UK as a cheap retrofit fish passage solution for low-head sloping weirs.

2. Materials and methods

2.1 Study area

This study was conducted on two streams in the River Ribble catchment (1133 km^2), one of the main river basins in northwest England. The Ribble drains limestone bedrock in its headwaters, running south and then west before flowing in to the Irish Sea. The two study streams were Swanside Beck (~100 m.a.s.l.), a minor tributary (5-12 m wide at study site) of the Ribble, and Chipping Brook (~150 m.a.s.l.), a minor tributary (5-10 m wide at study site) of the River Loud (Fig. 1). Both streams have substantial but recovering salmonid populations, including anadromous elements, with typical juvenile trout densities of 7.4 - 63.3 100 m^{-2} (Swanside Beck) and 33.0 – 66.8 100 m^{-2} (Chipping Brook) (M. Forty unpublished data). Both streams have riparian landscapes that predominantly consist of grassland which is subject to dairy and sheep farming. The substratum is predominantly composed of gravel, pebbles and cobbles in both streams. Swanside Beck runs for 6 km with moderate gradient (*ca.* 12.2 m km^{-1}) impeded by three low-head obstacles (< 3 m) (Fig. 1) while Chipping Brook runs for 4.5 km with a higher gradient of *ca.* 42.6 km m^{-1} and has six low-head obstacles (Fig. 1). A total of five structures were assessed across the two years, three on Swanside Beck and the first and second on Chipping Brook (Fig. 1). Of these, four were recently constructed fish passage structures: two pool-weir (PW1, PW2) traverse fish passes, one embedded rock ramp (ERR; large cobbles densely embedded in concrete), and one low-cost baffle (LCB) pass (Table 1, Fig. S1). The other structure was an unmodified open (uncovered) culvert (C) which was used as a control, contextualising observations at fish passes (Cooke & Hinch, 2013), representing a man-made structure which might pose a minimal barrier impact being well within expected swimming performance of brown trout (Table 1, Fig. S1) (Beamish, 1978; Tudorache et al., 2008).

2.2 Passive integrated transponder (PIT) logging stations

PIT telemetry was used to measure passage metrics of tagged trout at instream structures. Each site was monitored using a logging station comprising either two half-duplex (HDX) readers (Texas Instruments S2000, USA) in a master-slave configuration (Castro-Santos et al., 1996) and data logger (Flinka Fiskar, Sweden), or a Texas Instruments HDX multiple antennae reader and data logger (Oregon RFID, USA). These configurations interrogated each antenna 8 and 6 times per second respectively via a tuning unit connected to the logger. Two antennae loops (6 mm multi-stranded high quality copper speaker cable, 777 x 0.1 mm strands) were constructed across the stream channel at the downstream and upstream extents of each structure, interrogating the full stream width and depth, such that the direction and success of passage by individuals could be identified. Each loop was tuned to maximum detection range and efficiency. Tests with pole-mounted 12 mm and 23 mm tags were carried out by passing the tag through the loop at speeds of 1-1.5 ms^{-1} to simulate burst-swimming fish. In addition, PIT loop detection efficiencies were measured by calculating the proportion of tagged fish per array which were detected at the downstream antenna that were also detected upstream antenna as well as, where possible, the proportion of fish detected at the upstream antenna of an array that were also detected at PIT sites further upstream. Logging stations were powered using two 12 V, 110 Ah deep-cycle leisure batteries, run in parallel, which were changed every 3-4 days to avoid power supply failure. Data was downloaded at each battery change and the antennae loops tested as described above to ensure they were functioning correctly.

Four structures (C, PW1, PW2, LCB) were studied during summer-autumn 2013 using a two-part methodology investigating passage for naturally migrating trout in addition to utilising the homing instinct of individuals through displacement experiments. At each structure, fish (mostly parr and some adult freshwater-resident 'brown' trout) were first captured by electric fishing (pulsed DC Electracatch WFC4, Wolverhampton, UK and 1 KVA Honda generator), tagged and released where they originated within sections of a reach *ca.* 10-180 m downstream of the structure (Table 2). These fish were then monitored for between 13 and 21 days (Table 2). Following this, fish were captured in the first 100 m upstream of the structure, tagged and displaced 100 m downstream of the structure invoking a homing response (Armstrong & Herbert, 1997) but not inflated attraction values (Cooke & Hinch, 2013). In addition fish were tagged on the same day 100-200 m upstream of each structure, but released there and free to move to sites further upstream during migration. During autumn, opportunistic electronic fishing was carried out in pools in reaches up to 2 km downstream of the structures, in order to capture upstream-migrating adult freshwater-resident ('brown') and anadromous ('sea') trout. Logging stations ran until mid-December (Table 2) by which time naturally upstream-migrating individuals were expected to have completed spawning.

PW2 (Chipping Brook) was modified in early summer 2014 to correct an erroneous 0.37 m difference between the head drop at the first notch and that at the most upstream notch of the pass to 0.25 m between each pool (Table 1). A new embedded rock ramp (ERR) was also constructed on a flat-faced weir 20 m upstream of PW2 at the same time. Both of these structures were investigated in summer 2014 along with repeat studies of the LCB and C on Swanside Beck. All sites monitored in 2014 were subject only to short term displacement experiments conducted using the same format as in 2013 but with monitoring of the logging stations for the first 15 days following displacement as 73% of displaced fish in 2013 at LCB were detected attempting passage within this period (71-88% for fish passes in 2014). As PW2 and ERR were in close proximity, fish were captured above ERR and then displaced 100 m below PW2 using the same displacement group to test both structures.

PIT stations ran continuously during experiments with the exception of PW1 (13:00 12 Sept 2013 – 18:00 16 Sept 2013) and PW2 (12:00 12 Sept 2013 – 18:30 16 Sept 2013) which both experienced equipment failure at the beginning of displacement experiments. PIT antennae were washed out of the control culvert on 21 Oct 2013 and water levels then remained too elevated to re-install loops within reasonable time so monitoring was ceased at that point.

2.3 Experimental fish

Captured fish were placed in to covered reservoirs providing aeration and circulation by means of a 12 V submersible aerator pump (1732 L hr^{-1}). Trout were PIT tagged with one of two tag sizes depending on whether their fork length was between 80 and 130 mm (12 x 2.12 mm, 0.1 g) or greater than 130 mm (23 x 3.65 mm, 0.6 g) based upon Larsen et al. (2013). Prior to tagging fish were immersed individually in an anaesthetic bath of 2-phenoxyethanol (250 µL L^{-1}) until they reached stage III anaesthesia (McFarland, 1959). Fish were then measured (fork length), classed by phenotype and life stage (juveniles with parr marks, not expressing gametes; freshwater-resident 'brown' trout without parr marks; anadromous 'sea' trout without parr marks but silvered body) and a PIT tag inserted in to the peritoneal cavity via a 3-5 mm incision on the ventral surface anterior to the pelvic girdle. The incision was left un-sutured as studies have indicated this not to be necessary for small incisions (Bolland et al., 2009; Larsen et al., 2013). Tagged fish were placed in a recovery reservoir of aerated fresh water for observation ensuring they were able to maintain equilibrium and were responsive to external stimuli before release.

2.4 Environmental data

Water stage (level) and temperature were recorded on Swanside Beck and Chipping Brook in pool habitat 5 m upstream of the LCB and PW2 structures respectively. These were measured at 15 minute intervals using an automatic logger (HOBO U20-001-01-Ti; accuracy: 0.05 cm, 0.044^{o}C from 0^{o}-50^{o}C) placed in a stilling well affixed securely upright at the bank. Water level was then calibrated using a single point reading of depth at the data logger and hourly mean barometric pressure readings from a weather station at Bingley (53.81 N 01.87 W). The engineered structures were surveyed by measuring water depth and velocity in and immediately below each structure at base flow. Water velocity was measured using an electromagnetic velocity meter (Valeport, model 801) over 10 seconds, calculating the mean and standard deviation at 0.6 of the depth. At pool-weir type structures measurements were taken across the channel from 1 m downstream of each notch and at three equally spaced points in three cross sections within each notch. Measures were taken at LCB from 1 m downstream of the structure and then in the middle of the break in each set of baffles. In C, measurements were taken at 0.25 m increments across transects beginning 1 m downstream of the entrance, at the entrance and then at 2 m intervals.

2.5 Data analysis

In order to assess performance for fish passage at each structure several metrics were calculated. *Passage efficiency* was defined as the percentage of fish which successfully ascended a structure compared to those which were detected at the downstream antenna loop, attempting to ascend. *Proportion of Displaced fish Attempting Passage* (PDAP) was defined as the proportion of fish which attempted to ascend a structure compared of those which were displaced below it (note that this is not the same as attraction efficiency in many studies [Cooke & Hinch, 2013], but it is a useful metric of motivation of fish seeking to pass an obstacle to return to their home area). *Time to passage* was measured as the time between first detection at the downstream loop and the first detection at the upstream loop of a structure. An additional measure of passage delay impact was calculated, the *number of attempts* made by a fish before successful passage, where an attempt is defined as detection at the downstream antenna, not within 5 minutes of a previous detection. Data presented are the first recorded ascents of individuals and do not consider repeat ascents from fish which have fallen back downstream. Five fish (2% at PW1 and 1% at PW2 of those detected) included fish pass vicinities within their home range and persistently moved between the lower and upper antenna over multiple days. These fish were excluded from analysis. Non-parametric testing was used to compare these passage metrics between structures.

The effect of body length on the passage success of trout at structures was tested using binary logistic regression. This provides a useful method for modelling a binary response variable (successfully or unsuccessfully ascending a structure) based on a predictor variable (length) (Bewick et al., 2005; Starrs et al, 2011). Models were constructed using 2013 data and tested for significance against the Null model. A model for 2014 PW2 after modification was constructed for comparison to 2013 PW2. Logistic regression was not fitted where complete separation arose due to 100% passage efficiency (Field, 2005). All analyses were conducted using R version 2.15.2 (R Core Team, 2012).

3. Results

3.1 Migration and passage efficiency

A total of 845 and 337 trout were PIT tagged in 2013 and 2014 respectively across the two study streams, with fork lengths ranging from 80 – 450 mm (Table 2). In situ detection efficiencies of tagged fish averaged 98.5% for upstream antennas and 94.9% for downstream antennas, for all five sites and both years. On Chipping Brook, the proportion of non-displaced parr morphotype trout detected attempting to move upstream was 29% (*n* =137) of which 38% were successful at PW2. On Swanside Beck the proportion of non-displaced trout of parr morphotype exhibiting upstream movement was 32% (*n* = 278) of which 100%, 56% and 65% were successful at C, LCB and PW1 respectively. Of these, the proportion moving from downstream of C was 15% (*n* = 32) to LCB and 13% to PW1. Of those tagged between C and LCB the proportion moving upstream to PW1 was 10% (*n* = 108).

Of the four structures investigated in 2013, passage efficiency for trout was observed to be highest at the control C (100%; Table 3) as expected. Within the three fish passes highest overall passage efficiency (from displacement and non-displaced samples combined) was observed at PW1 (76%) followed by the LCB (68%; Table 3). Passage efficiency values for PW1 and PW2 are minimums due to short periods of PIT logger down-time. In 2014 the LCB demonstrated the best passage efficiency (82%, Table 4) of the three fish passes studied, with the control culvert again exhibiting near complete passage efficiency (96%). Of the two cumulative structures in close proximity the most downstream of them, PW2 (79%), recorded a higher passage efficiency than the ERR (71%). The LCB structure was also more efficient in 2014 than 2013 (Table 4) in displacement experiments by 15%.

In long-term experiments in 2013 the Proportion of Displaced fish Attempting Passage (PDAP) was highest at the LCB (91%; Table 3), much higher than for the control culvert (51%), characterised by a large, deep pool immediately downstream. Within the 15-day displacement experiments PDAP was higher in 2014 for C and the LCB which were studied in both years (Table 2). PDAP was very similar between PW2 (87%) and the LCB (88%) in 2014, with the ERR having a lower value than PW2 immediately downstream of it.

Stage and water temperature data from 2013 (Fig. 2) and 2014 (Fig. 3) are displayed in relation to cumulative passage success. During fish displacement experiments on Swanside Beck water level was slightly but significantly higher in 2013 than 2014 (Independent t-test, $t = 6.43$, df = 2768.1, $P < 0.001$) and water temperature was *ca.* 3^{o}C lower in 2013 than 2014 ($t = -77.70$, df = 4099.78, $P < 0.001$). This was also found to be the case on Chipping Brook during fish displacement experiments for water level ($t = -18.88$, df = 2484.62, $P < 0.001$) and temperature ($t = -30.57$, df = 2901.09, $P < 0.001$) between 2013 and 2014.

3.1 Delay before successful passage

In the 2013 long-term migration experiments, significant differences were found in time to passage between the four structures (Kruskal-Wallis test, H (3) = 54.7, P < 0.001) as well as in the number of attempts (Kruskal-Wallis test, H (3) = 68.5 , P < 0.001). Time to passage was shortest at control C (median = 0.70 h; Fig. 4) and longest at PW2 (median = 127.22 h). Time to passage at each structure in long-term experiments was significantly different from the control C with the exception of PW1 (Mann-Whitney test, U = 774, P < 0.31; Fig. 4). Significant differences were also found in displacement experiments between structures, for time to passage (Kruskal-Wallis test, H (4) = 42.2, P < 0.001; Fig. 5) as well as number of attempts (Kruskal-Wallis test, H (4) = 24.5, P < 0.001). Though C still provided the shortest passage time in 2014 displacement experiments ($median_{2014}$ = 0.51), longest passage times were experienced at the LCB in 2013 (median = 4.01 h) but were notably, though not significantly, shorter in 2014 (median = 0.97 h). Time to passage was also significantly shorter at PW2 in 2014 (median = 2.37; U = 2740, P < 0.001) following adjustments in its construction after long delays were observed in long-term experiments in 2013 (median = 108.29 h). Of the fish passage structures the ERR provided the least impact both in terms of time to passage and number of attempts (median = 0.66 h and 1 respectively).

As with time to passage passage, the number of attempts before successful passage was lowest at C (median = 1; Fig. 4) and greatest at PW2 (median = 7). Number of attempts was significantly greater for all structures compared against control C (Fig. 4) in long term experiments, while only the LCB exhibited significantly higher numbers of attempts before successful passage in comparison with C in displacement experiments in 2013 (U = 1075, P < 0.02) and 2014 (U = 1050, P < 0.01).

3.2 Fork-length and passage success

Significant logistic regression models ($P < 0.05$) were created for three structures (LCB, PW1, PW2) based on data from long-term experiments collected in 2013 (Fig. 6, Table 5) and the displacement data from 2014 for PW2 following its alteration. Although the 50% probability of passage (P_{50}) did not differ significantly between fish passes, the models suggest that PW1 functioned best for smaller trout, with a P_{50} for a length of 91 mm (Fig. 6). Of the other two structures $PW2_{2013}$ (P_{50} = 132 mm) performed worse than the LCB (P_{50} = 113 mm) for smaller fish. All structures had a P_{90} under 250 mm with PW1 (P_{90} = 199 mm) showing evidence of better performance than LCB (P_{90} = 222 mm) and PW2 (P_{90} = 222 mm). After alteration, $PW2_{2014}$ showed an increase in performance for all lengths of fish (Fig. 6, Table 5), outperforming the other structures for smaller fish (P_{50} = 82 mm, P_{90} = 192 mm). A significant model could not be constructed for the control culvert C due to complete separation arising from 100% passage efficiency and the model for ERR was insignificant.

4. Discussion

This study provides field evidence of the varying performance of three fish passage designs for upstream passage of both juvenile and adult *Salmo trutta* at low-head barriers and the variation in delay that can be incurred even between similarly designed passes. We provide the first passage efficiency measurements (67-82%) of a low-cost baffle (Servais, 2006) fish pass for trout of a wide range of sizes. This performed quite similarly in terms of passage efficiency to the other fish pass designs tested, even though operating at nearly double the gradient (24% vs 12% in our study; Table 1).

Predictive models suggested that passage success was closely related to fork length of individuals with probability of passage reduced for smaller fish. About 30% of tagged parr released at their capture site attempted passage at one or more structures and this, as well as upstream dispersal and homing demonstrates that small (including juvenile), as well as large adult trout need to be considered in terms of effective upstream passage provision. Additionally short-term displacement experiments of resident trout combined with PIT telemetry was identified to potentially provide a rapid performance assessment tool for determining trout passage at structures and to aid fine-tuning of fish pass modifications.

Passage efficiencies observed at fishways in this study were all below the minimum 90% target that recommended as a minimum for sustaining and recovery of populations of diadromous and markedly potamodromous species (Lucas and Baras, 2001), but well above the average passage efficiency (48%) recorded in a large meta-analysis by Bunt et al. (2012).Only control C, a 20 m culvert with 4% slope, exceeded the minimum 90% passage efficiency target (96-100% passage efficiency) with water velocities which were well within the swimming performance abilities of *S. trutta* (Beamish, 1978; Tudorache, 2008; Videler, 1993). In addition to this, passage efficiencies were found to be variable between and within design types with differences also observed across years. Bunt et al. (2012) reported that passage efficiency varied broadly across a range of fishway types when conducting a meta-analysis of 19 studies of 26 species at instream barriers to migration. Where fish had to pass two structures in close proximity at PW2 and then the ERR both passage efficiency and PDAP were lower at the upstream structure, despite shorter passage time and lower number of attempts at the ERR. Due to the close proximity of these structures it is hard to discern whether this result is influenced more by the individual design of the structures or whether the energy expended in passing the first structure reduces a fish's motivation to attempt the second or impacts the likelihood it will pass both structures. Given this, the values for passage efficiency and PDAP at ERR may be considered conservative values. Cumulative barriers to migration can potentially have substantial effects on upstream passage even when individual structures pose what seem to be a negligible impact (McKay et al., 2013).

In this study 50% probability of successful upstream passage at fishways was associated with lengths representative of trout in the 1+ age cohort for this catchment (80 – 132 mm; M. Forty, unpublished). Swimming capacity has been shown to be a factor of body length (Beamish, 1978; Videler, 1993). Tudorache et al. (2008) suggested, based on flume experiments, that maximum flow velocity in culverts for brown trout of fork length 78 ± 2 mm at 15^{o}C should be 0.45 ms^{-1}. High passage success was observed at the control culvert despite having higher base flow velocities at the entrance than this recommendation (0.80 ms^{-1}). This may be explained by trout having been able to use burst swimming to enter the structure and then utilise local flow refugia while moving through the culvert, where the observed mean velocity was lower (0.46 ms^{-1}). High passage efficiencies have been previously observed in nature-like fishways characterised by high maximum water velocities for both weak (Calles & Greenberg, 2007) and strong (Calles & Greenberg, 2005, 2009) swimming species. Successful passage of some individuals at fishways with locally high velocities may be indicative of their strong motivation to pass upstream and their abilities in the wild to outperform maximum swimming speeds observed in confined flumes (Haro et al., 2004; Peake & Farrell, 2004). The use of flow refugia may also partially explain the high passage success observed at LCB and ERR, where sustained swimming at higher velocities (mean = 1.42 and 1.13 ms^{-1}) is required as these pass types lacked well-defined resting areas as provided by pool-weir type passes. The short length of these structures (< 10 m) will also contribute to a moderately high passage success of small fish in our studies; reducing the duration of swimming at these velocities and allowing fish with a greater range of swimming abilities to pass.

Creating fish passage structures in small streams so that they are passable by juvenile fish as well as adults would allow for recovery of populations following disturbance events such as high stream flows or pollution incidents, and would also facilitate upstream dispersal. High stream flows can result in the displacement of juvenile salmonids downstream of structures impacting their survival (McMahon & Hartman, 1989; Ottaway & Clarke, 1981) where they may end up in unsuitable habitats such as deeper pools potentially increasing susceptibility to predation from larger piscivorous fishes, or in juvenile habitat with increased population density due to displacement, generating increased intraspecific competition causing density-dependent fitness impacts. Our displacement experiments mimicked such upstream movements. Mature parr morphotype salmonid males (precocious parr) have been identified to contribute towards spawning success of populations (Dellefors & Faremo, 1988; Garcia-Vazquez et al., 2001; Hutchings & Jones, 1998). In this study *ca.* 30% of non-displaced parr morphotype trout were observed to exhibit upstream movement in both study streams in 2013 with a number of those tagged below the most downstream site on Swanside Beck observed passing over 3 km upstream through all three structures during the autumn. We hypothesise these individuals were mature male parr.

While the site-specific displacement experiments were comparable in terms of the monitoring duration following displacement, there were limitations in resource availability precluding exactly simultaneous experiments and there were also differences between sites in the availability of fish of different sizes for tagging. Improved passage efficiency at C and the LCB in 2014 may have been due to significantly higher stream temperatures (approximately 3°C higher for Swanside Beck and 1°C higher for Chipping Brook) in 2014 compared to 2013 during the displacement experiments. Water temperature may influence swimming capacity of fish as it has been found to affect the muscle contraction speed of fish (Beach, 1984; Wardle, 1980). However, brown trout swimming performance was observed to be similar in summer (15°C) and winter (5°C) as long as fish had acclimatised to those temperatures by Day & Butler (2005). Also, Jain & Farrell (2003) demonstrated that rainbow trout (*Oncorhynchus mykiss*) performed better acclimated at lower temperatures (ca. 5°C) than higher temperatures (*ca.* 17°C) in a repeated swimming performance experiment.

Each of the structures studied were designed and constructed across the width of the stream to maximise attraction flow, and as such did not have to compete for attraction flow as would occur for a fish pass at a large dam or main river weir (e.g. Gowans et al., 1999). Despite this there was much variation in PDAP between structures during displacement experiments, being higher for fish passes (71 – 88%) than for the control culvert (49%) in 2014 (Table 4). The habitat characteristics created in areas downstream of instream structures could be a potential factor in determining the motivation for displaced fish to approach and attempt to pass a structure; C had a constrained surface-positioned entrance above a large, deep scour pool, which may have limited attraction, even though the whole of the stream flow entered via C. While plunge pools and dam tailwaters, supplied with well oxygenated water and an abundance of food can provide propitious habitats for a number of fish species, they may also have the potential to reduce motivation for smaller fish to pass through them due to exposure to predation from larger piscivorous fishes that reside in deeper pool habitat (e.g. Schlosser, 1987). The lower PDAP values observed at PW1 and PW2 in 2013 are likely an artefact of data loss due to equipment failure in the period directly after displacement in that year.

Time to passage was found to be highly variable between structures. Passage times were slightly shorter within displacement experiments than long-term experiments, likely because of the shorter duration of monitoring post-displacement biasing towards fish which may have a greater motivation to pass upstream than ones which wait longer before attempting. As with improved passage efficiency, the LCB structure also showed improved performance in terms of reduced time to passage in 2014 compared with 2013, perhaps due to increased temperature in 2014 experiments. The improvement works on PW2 between 2013 and 2014 appear to have been successful in addressing the issues with long delays, suggesting that these were due to conditions caused by the unsuitable head drop at the entrance notch to the structure. In addition to providing a complete barrier for some individuals, delays incurred at instream structures during upstream passage can have detrimental impacts on spawning success and survival where the excessive energy expenditure interferes with physiological and behavioural processes (Mesa et al., 2003) and increases the risk of predation (Peake et al., 1997; Rieman et al., 1991). In situations where fish have to pass multiple in-stream structures these effects can be compounded, threatening survival of anadromous populations and potentially driving facultatively anadromous species such as *Salmo trutta* towards resident-dominated populations (Baras & Lucas, 2001).

While the passage efficiencies of fishways in this study did not attain the minimum 90% target recommended by Lucas and Baras (2001), the study areas were dominated by spawning and nursery habitat, and therefore such high passage efficiencies may be unnecessary to sustain the population and key processes such as dispersal and migration. Further, due to the size-selective effects of the fish passes, larger adults (> 30 cm), with high fecundity, did have passage efficiencies above 90% for all pass types for which size effects could be modelled. Nevertheless, supporting passage for the full range of life stages and sizes within populations may be important; for salmonids the emphasis on upstream pass provision is normally for large adults only, because (especially for females) these have high fecundity and economic value, but this ignores the wider functionality of upstream movements in juveniles and small adults. Our results suggest that in tributaries for salmonid spawning, greater consideration should be made towards facilitating naturally occurring upstream migration and dispersal of juvenile morphotype salmonids.

This study identifies that field studies are a vital component of evaluating and optimising fish pass effectiveness, informing management decisions. This is demonstrated by improvements in passage observed in 2014 following the actions that could be taken after the identification of long delays incurred at Pool-Weir 2 during 2013 in this study. The number of fish passage structures which have been evaluated in relation to the large number constructed globally is very small (Schmutz et al., 1998). This is particularly true of low-head instream structures present within smaller streams (Alexandre & Almeida, 2010; Ovidio & Philippart, 2002). As demonstrated in this study, there is a wide variation in performance between and within fish pass designs, especially in terms of passage efficiency for different life stages and in the delays which can be incurred even between similarly designed structures. This indicates that as much as improved understanding of factors influences the effectiveness of fish passes, detail needs to be paid to the build quality of technical passes.

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Figure legends

Fig. 1. Map of study area with in-stream structures shown as black circles (top and bottom right).

Fig. 2. Mean daily stage (solid-black) and mean daily water temperature (solid-grey) plotted with the cumulative proportion of successful fish in 2013 on Swanside Beck (left) for Culvert (dashed), Low-Cost Baffle (dotted) and Pool-Weir 1 (dot-dash), and Chipping Brook (right) for Pool-Weir 2 (dashed). Arrows indicate dates of displacement respectively.

Fig. 3. The cumulative proportion of successful fish in displacement experiments in 2014 on Swanside Beck (left) for Culvert (dashed) and Low-Cost Baffle (dotted) structures and Chipping Brook (right) for Pool-Weir 2 (dashed) and Embedded Rock Ramp (dotted) fish passes plotted with mean daily stage (solid-black) and mean daily water temperature (solid-grey).

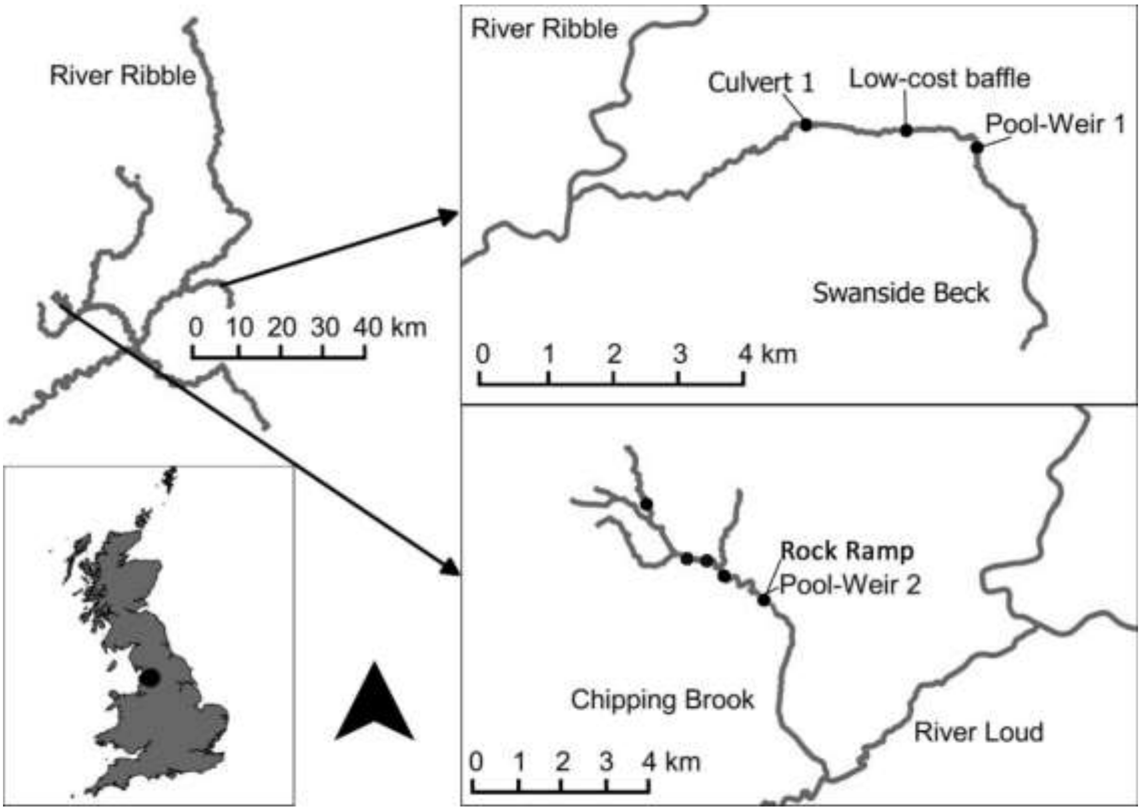
Fig. 4. Boxplots of the passage time (h) and number of attempts before successful passage for long term experiments in 2013. Boxplots display the median, 1st and 3rd quartiles and the 95% confidence interval of the median with outliers. Pairs not joined by the same letter represent where there were significant differences between structures (or years). Delays and attempts were analysed separately as were long term and displacement experiments (Mann-Whitney *U* test with Bonferroni corrected significance at $P < 0.035$).

Fig. 5. Boxplots of the passage time (h) and number of attempts before successful passage for short term displacement experiments (2013 and 2014). Boxplots display the median, 1st and 3rd quartiles and the 95% confidence interval of the median with

outliers. Pairs not joined by the same letter represent where there were significant differences between structures (or years). Delays and attempts were analysed separately as were long term and displacement experiments (Mann-Whitney *U* test with Bonferroni corrected significance at $P < 0.035$).

Fig. 6. Logistic regression models for LCB, PW1 and PW2 in 2013 and after alteration in 2014 showing predicted probability of passage of an individual based on its length and ultimate passage success data collected during study with 95% confidence intervals (grey area). All models significant against the Null model at $P < 0.05$.

Figures



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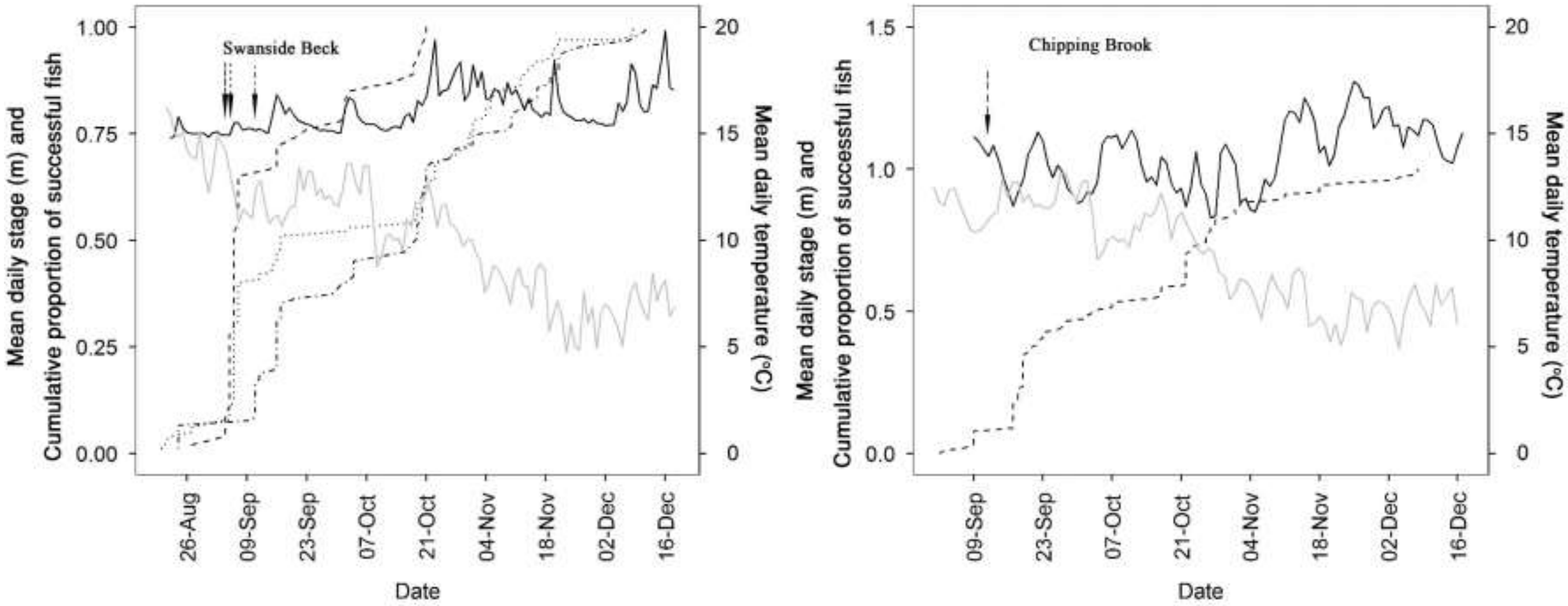

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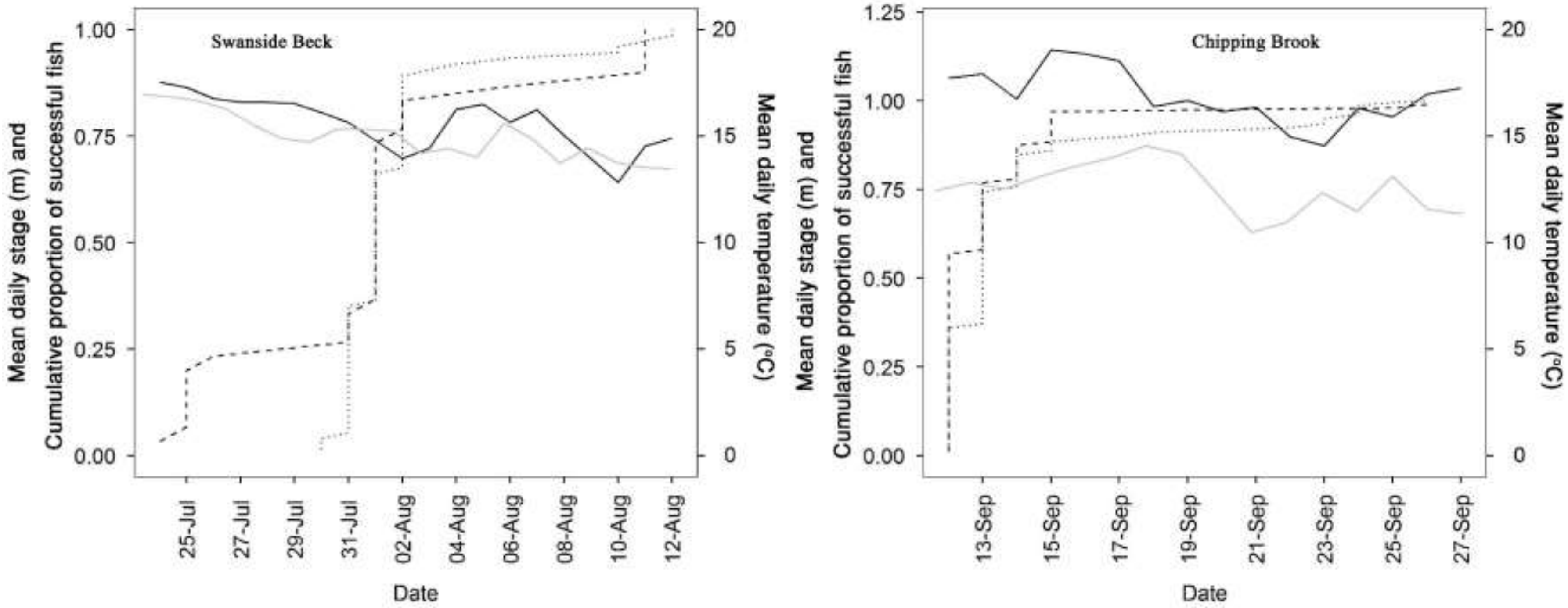

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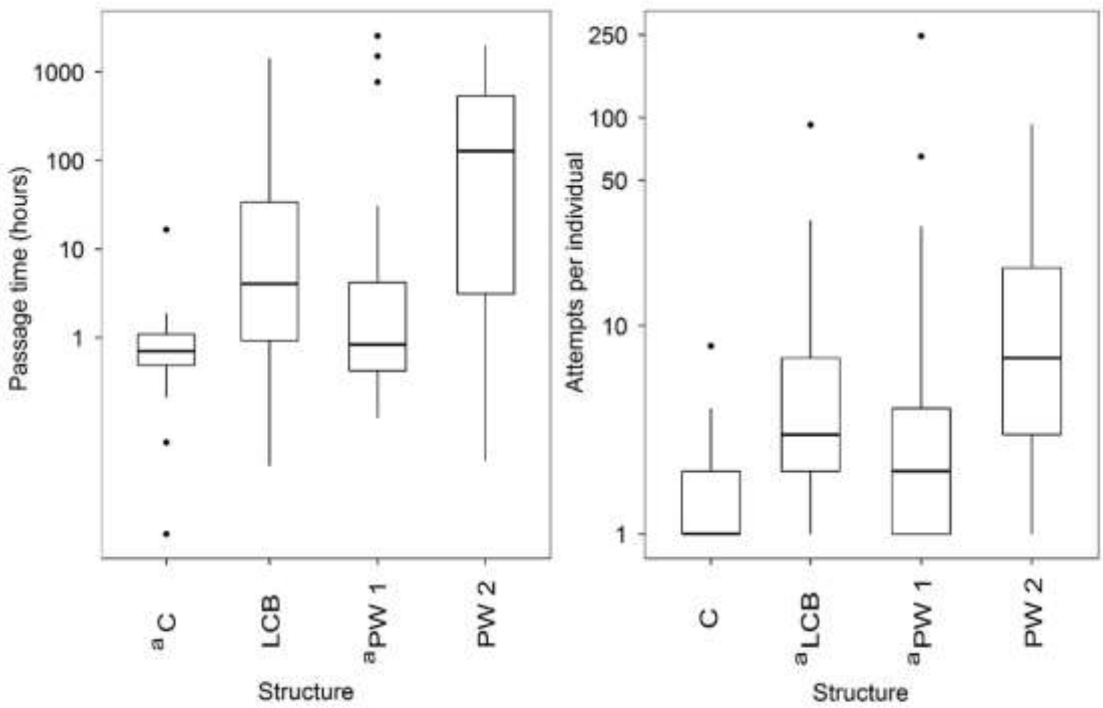

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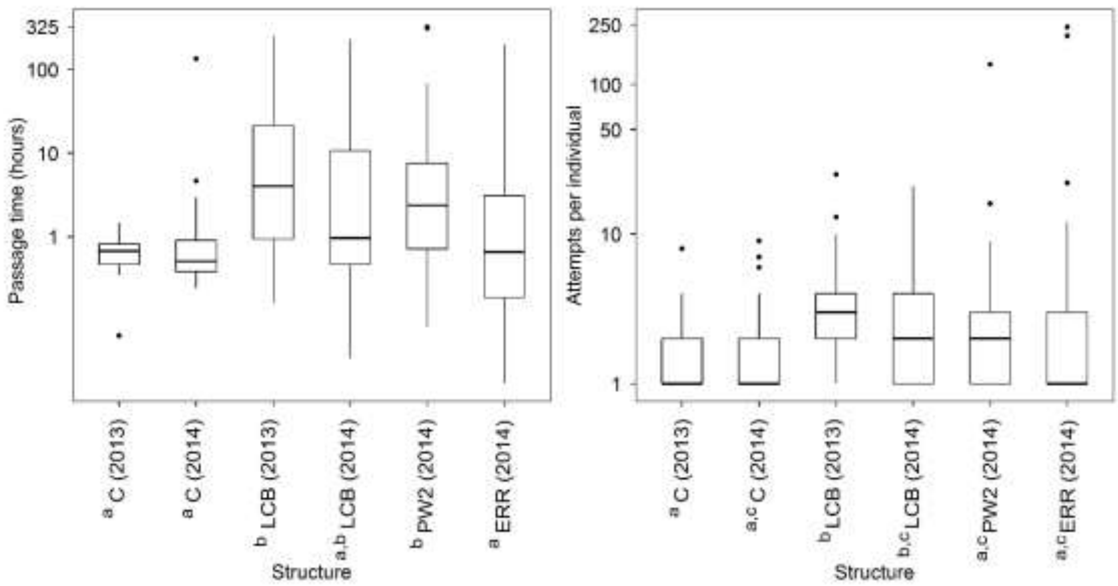

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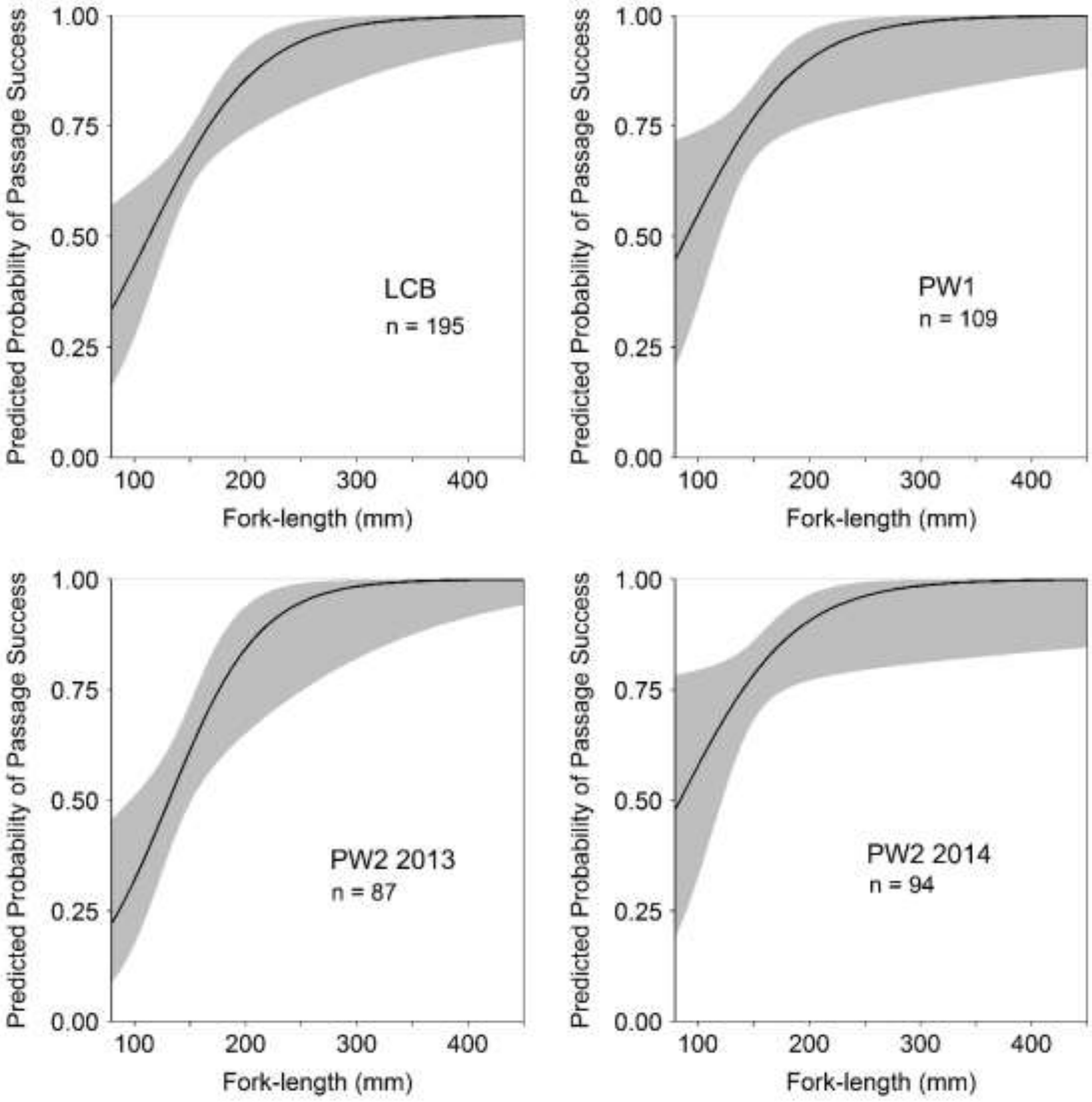

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Tables

Table 1

Physical characteristics of studied structures.

	Culvert (control)	Fish passes				
		Low-cost baffle	Pool-Weir 1	Pool-Weir 2 (2013)	Pool-Weir 2 (2014)	Embedded Rock Ramp
Length (m)	20	6.70	8.43	7.20	7.20	4.57
Width (m)	0.50	7.6 - 9.7	6.20	8.65 - 10.50	8.65 - 10.50	6.80
Head (m)	0.80	1.60	1.16	0.84	0.84	0.55
Slope (%)	4%	24%	12%	12%	12%	12%
Mean base flow velocity at entrance (ms^{-1})	0.80	1.85	1.87	1.97	1.91	1.28
Mean entrance depth at base flow (m)	0.12	0.15	0.06	0.10	0.10	0.30
Mean velocity in structure (ms^{-1})	0.46	1.42	0.45*	0.84*	0.78*	1.13
Notch width (m)	-	0.35	0.60	0.60	0.60	-
Baffle height (m)	-	0.20	-	-	-	-
Pool step height (m) downstream, upstream	-	-	0.25-0.33	0.49, 0.23, 0.12	0.25	-
Number of pools	-	-	3	3	3	-
Number of notches	-	16	4	4	4	-

*based on measures in flow entering pools from notches at transects 0.5 and 1 m away from notch.

Table 2

Summary of experimental groups of *Salmo trutta* PIT tagged during 2013 and 2014.

Source	Date	Number tagged	Length [mean SD (range), mm]
Swanside Beck			
Culvert downstream	19/08/2013	33	163.9 ± 35.3 (101 - 266)
Culvert upstream	04/09/2013	12	128.1 ± 38.0 (82 - 191)
Culvert displaced	04/09/2013	68	119.7 ± 34.8 (82 - 191)
	24/07/2014	53	152.4 ± 42.4 (80 - 294)
Low-cost baffle downstream	20/08/2013	101	154.5 ± 24.1 (114 - 233)
Low-cost baffle upstream	05/09/2013	49	133.0 ± 31.6 (80 - 213)
Low-cost baffle displaced	05/09/2013	118	148.2 ± 28.9 (83 - 298)
	30/07/2014	101	154.5 ± 34.1 (112 - 293)
Pool-weir 1 downstream	21/08/2013	93	127.3 ± 21.3 (94-211)
Pool-weir 1 displaced	11/09/2013	72	130.8 ± 29.7 (80 - 208)
Swanside Beck supplementary migrants			
Culvert downstream	19/09/2013	5	222 ± 30.4 (191 - 256)
	28/10/2013	1	425
	06/11/2013	1	450
	12/11/2013	4	329.3 ± 80.7 (220 - 410)
	22/11/2013	1	413
Total Swanside Beck	**2013**	**558**	**142.4 ± 42.6 (80 - 450)**
	2014	**158**	**156 ± 39.3 (80 - 294)**
Chipping Brook			
Pool-weir 2 downstream	30/08/2013	146	135.0 ± 38.3 (80 - 254)
Pool-weir 2 displaced	12/09/2013	141	159 ± 51.6 (109 - 443)
Pool-weir 2 and Embedded Rock ramp displaced	12/09/2014	179	145 ± 40.6 (102 - 326)
Total Chipping Brook	**2013**	**287**	**153.4 ± 49.0 (80 - 443)**
	2014	**179**	**145.0 ± 40.6 (102 - 326)**

Table 3

Passage success of *Salmo trutta* during long-term experiments in 2013. Proportion of Displaced fish Attempting Passage (PDAP) values are calculated for trout displaced from upstream to below the structure only; these fish may be expected to attempt to return home.

	C	LCB	PW1*	PW2*
Number displaced	68	128	73	139
Number attempted				
Displaced	35	117	48	119
Non-displaced	7	78	61	87
Total	42	195	109	206
Passage efficiency (%)				
Displaced	100	74	79	53
Non-displaced	100	63	74	59
Total	100	68	76	55
PDAP (%)	51	91	66	86

*Minimum estimates of attempts, passage efficiency and PDAP due to 4-day (3.4 – 3.8% of total experiment duration) periods of equipment failure shortly after fish displacement; measures of non-displaced fish passage efficiency are expected to have been least affected.

Table 4

Passage success of *Salmo trutta* within 15 days following displacement below structures in 2013 and 2014 showing passage efficiency and Proportion of Displaced fish Attempting Passage (PDAP).

	2013				2014			
	C	LCB	PW1*	PW2*	C	LCB	PW2	ERR
Number displaced	68	128	73	139	53	101	178	154
Attempted	25	94	48	52	26	89	154	109
Succeeded	25	63	38	37	25	73	121	77
Passage efficiency (%)	100	67	79	71	96	82	79	71
PDAP (%)	37	73	66	37	49	88	87	71

*Minimum estimates of attempts, passage efficiency and attraction efficiency due to 4-day (26% of total experiment duration) periods of equipment failure shortly after fish displacement

Table 5

Summary of logistic regression models of length and successful passage based on long-term observations in 2013 and 15-day displacements in 2014.

Site	Coefficient	Std. Error	z statistic	*P* <	Wald test $\chi 2$	df	*P* <	Likelihood ratio test	df	*P* <
LCB_{2013}	0.02	0.007	2.998	0.003	9	1	0.003	13.672	1	0.0002
P-W 1_{2013}	0.02	0.009	2.331	0.02	5.4	1	0.02	7.8	1	0.005
P-W 2_{2013}	0.02	0.008	2.977	0.003	8.9	1	0.003	13.669	1	0.0002
P-W 2_{2014}	0.02	0.009	2.121	0.03	4.5	1	0.03	6.30	1	0.01